THE VISCACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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VISCACEAE Batsch, Tab. Affinitatum Regni Veg. 240. 1802, "Viscinae."

(MISTLETOE FAMILY)

Shrubs or herbaceous perennials parasitic on a great variety of host plants, usually foliaceous with decussate [rarely alternate] phyllotaxy, the nodes showing constrictions, the plants thus appearing jointed. Leaves simple and often succulent [rarely squamate], persistent, estipulate, the margins entire. Mode of attachment simple, but haustorial organ usually much fragmented within host. Flower small and inconspicuously colored, actinomorphic, in spikes [or other inflorescences], imperfect, the plants dioecious [or some monoecious]. Perianth uniseriate, consisting of 3 or 4 members, fused with the inferior ovary; or with 1 stamen each and arranged around a central cushion. Anther variously constructed but usually sessile on a perianth member; pollen spheroidal, tricolporate, isopolar, and somewhat echinate. Stigma and style scarcely differentiated; ovarian cavity exceedingly inconspicuous, the ovules undifferentiated, the megaspore mother-cells arising from a centrally located papilla, the usually single seed, therefore, without a proper seed coat. Fruit a 1- (or 2-)seeded berry with viscid tissue surrounding a large chlorophylliferous endosperm and 1 (or 2) straight and poorly developed embryos. (Loranthaceae subfam. Viscoideae Engler, Nat. Pflanzenfam. III. **1:** 177. 1889. Excluding Loranthaceae A. L. de Jussieu, Ann. Mus. Natl. Hist. Nat. **12:** 292. 1808, "Lorantheae," nom. cons., and Eremolepidaceae Van Tieghem ex Kuijt.[2]) TYPE GENUS: *Viscum* L.

[1]Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation, under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 92nd in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets [ ].

The illustration of *Phoradendron* was begun in early January, 1964, by the late Dorothy H. Marsh (who drew parts a, b, and g) under the supervision of Carroll Wood, but because of Mrs. Marsh's failing health it could not be completed then. Much later, Karen Stoutenberger drew the remaining items from dissections made by Kenneth R. Robertson. The materials for the illustration were either living plants from Floyd County, Virginia, or alcohol-preserved specimens of these (a, b, g–l) and specimens from the Gray Herbarium (c–f, *Small, Mosier, & Small*, 1928, St. Lucie County; *Craighead, Popenoe, & Campbell*, 1963, Monroe County, Florida).

[2]**Eremolepidaceae** Van Tieghem ex Kuijt (Eremolepidacées Van Tieghem, Compt. Rend. Acad. Sci. Paris **150:** 1717. 1910, nomen invalidum; Eremolepidaceae Van

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A family of seven genera and 400 species, primarily tropical, but reaching well into Temperate zones on various continents. All genera but *Arceuthobium* Bieb. are restricted to either the New World or the Old. *Phoradendron* Nutt. is represented in our area by only two species, one widespread and the other in southernmost Florida. The only other North American genus of the family, *Arceuthobium*, dwarf mistletoe, is unknown from the southeastern United States, except as pollen in Pleistocene deposits in the Carolinas and Georgia (see Whitehead & Barghoorn and Watts). At present, the nearest station of the eastern dwarf mistletoe, *A. pusillum* Peck, which parasitizes *Picea mariana* (Miller) BSP., black spruce, and *P. glauca* (Moench) Voss, white spruce, appears to be some 500 miles to the north, in northern Pennsylvania. Other species of *Arceuthobium* are sometimes serious pests on conifers in western North America (see Hawksworth & Wiens).

The Viscaceae have been treated by various authors either as a family or as subfam. Viscoideae of the Loranthaceae, the other subfamily being the Loranthoideae. The small neotropical family Eremolepidaceae has frequently been regarded as part of the Viscaceae, but it warrants separate familial status on the basis of pollen (Feuer & Kuijt, 1978), the predominance of alternate phyllotaxy, and catkinlike inflorescences, as well as the occurrence of epicortical roots in two of its genera. Viscaceae and Loranthaceae are usually easily distinguished: the "showy mistletoes" belong to the Loranthaceae, while those with inconspicous flowers are usually members of the Viscaceae. In addition to the minute flowers with a single whorl of perianth members, the Viscaceae are characterized by a fruit with the viscous layer *within* the vascular bundles, a single embryo sac of the Allium type, an embryo with a very short suspensor or none, stamens opposite the perianth segments, the anther opening by pores or transverse slits, spherical pollen, a zygote in which the first cleavage is horizontal, and simple endosperm. In contrast, the Loranthaceae usually have perfect flowers with two perianth whorls (the outer one greatly reduced to a calyculus), a fruit with the viscous layer outside the vascular bundles, several embryo sacs of the Polygonum type, an embryo with a very long, multiseriate suspensor, stamens opposite the petals, anthers opening longitudinally, pollen mostly trilobate, zygote with the cleavage vertical, and compound endosperm.

Barlow (1964), in pointing out these differences, noted that "most of the characters that the two families have in common are also features of the Santalaceae, where hemiparasitism is common (mostly root parasitism) and there are various degrees of reduction and suppression of ovules and elongation of embryo sacs (Johri & Bhatnagar, 1961). It is most likely that the two groups have had independent origins from ancestral stocks in the San-

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Tieghem emendavit Kuijt, Brittonia **20:** 140. 1968, nomen invalidum).

Plantae parasiticae epiphyticae dioeciae radicibus epicorticalibus evanidis et foliis alternis. Inflorescentiae amenta vel spicae subtentae squamis imbricatis. Flores parvi sessiles monochlamydei; perianthium masculinum tri- vel quadripartitum; perianthium foemineum bi- vel tripartitum. Stamina 3 vel 4 distincti lobis perianthii opposita; antherae biloculares. Ovarium inferum (vel semisuperum). Fructus destitutus staminodia setiformes, textura viscida; endospermium viride; cotyledones embryonis duo. TYPUS: *Eremolepis* Grisebach.

talaceae, so that by placing them in a single family they constitute a diphyletic and therefore unnatural group. The new characters which the groups share are the aerial habit, which in fact has been discovered in several other families of Santalales and which therefore has probably originated several times, and the baccate fruits, which are a consequence of the aerial habit and of independent development. . . . The Loranthaceae and Viscaceae are thus relatively uniform groups characterized by a high degree of reduction in the ovary and by a hemiparasitic habit, these being features also of the Santalaceae, from which they have independently arisen." Kuijt (1968) has subsequently suggested that the Viscaceae and the Loranthaceae are derived from the Santalaceae and the Olacaceae, respectively. The Viscaceae extend into the Temperate Zones of Eurasia and North America, while the Loranthaceae are almost exclusively tropical and subtropical.

It is commonly accepted that mistletoe parasitism involves the transfer of water and inorganic materials from the host to the parasite, which synthesizes its own organic requirements. However, even squamate mistletoes such as *Arceuthobium*, which appear to lack chlorophyll, have at least some. This simple picture of mistletoe parasitism has been complicated considerably by the discovery of the transfer of significant amounts of photosynthates from the parasite to the host—in a sense, an inversion of parasitism.

Host preference also appears to be exceedingly complex. Tropical mistletoes generally show little specificity as to host, although interesting exceptions do exist. If one scans the list of host records of a mistletoe of the Temperate Zone, such as *Phoradendron serotinum* (*P. flavescens*), one gains the impression of a similarly undiscriminating parasite. Lists of hosts, however, tend to obscure significant local differences in preference (see Baldwin & Speese under *Phoradendron*). The possibility of parasitic races seems to be a very real one, although genetic variability in the resistance of the host has too often been ignored as an alternative or additional possibility.

A remarkable embryological peculiarity seems to be restricted largely to the Loranthaceae. The megagametophyte in these plants is an intrusive structure that grows out into the carpel wall and up into the style. The height to which the megagametophyte ascends appears to provide a generic character of some taxonomic stability. It has been demonstrated in some that the megagametophyte may actually reach the stigmatic surface and thus be exposed to the air. Here the egg cell awaits fertilization, after which the proembryo is pushed back down the style to the original point of origin of the gametophyte. The megagametophyte thus seems to have usurped the function of the pollen tube. Unfortunately, the neotropical Loranthaceae are very poorly known in this respect. Members of the Viscaceae seem to have a more orthodox embryology, but apogamy has been reported in *Dendrophthora* Eichler.

The Viscaceae are characterized by two main chromosome groups, the first (including *Arceuthobium*, *Phoradendron*, and *Dendrophthora*) with $x = 14$, the second (*Viscum*) with $x = 10$, 11, 12, and 13 (Wiens & Barlow). There are significant cytological differences between the Viscaceae, the Eremolepidaceae, and the Loranthaceae (see also Barlow & Wiens).

Modern pharmacology has given a certain amount of credence to some of the mistletoe's early uses in folk medicine (see Gill & Hawksworth). Virtually all such work, however, is based on the European *Viscum album* L. Both *Phoradendron* and *Arceuthobium* are unimportant in the materia medica of North America. The berries of *Phoradendron* "contain toxic amines which cause acute stomach and intestinal irritation with diarrhea and slow pulse" (Hardin & Arena) or even death (see *Phoradendron*).

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Since opinion has differed with respect to the Viscaceae as a family or as subfamily Viscoideae of the Loranthaceae, a number of references that treat both or only the Loranthaceae (subfamily Loranthoideae) are included here.

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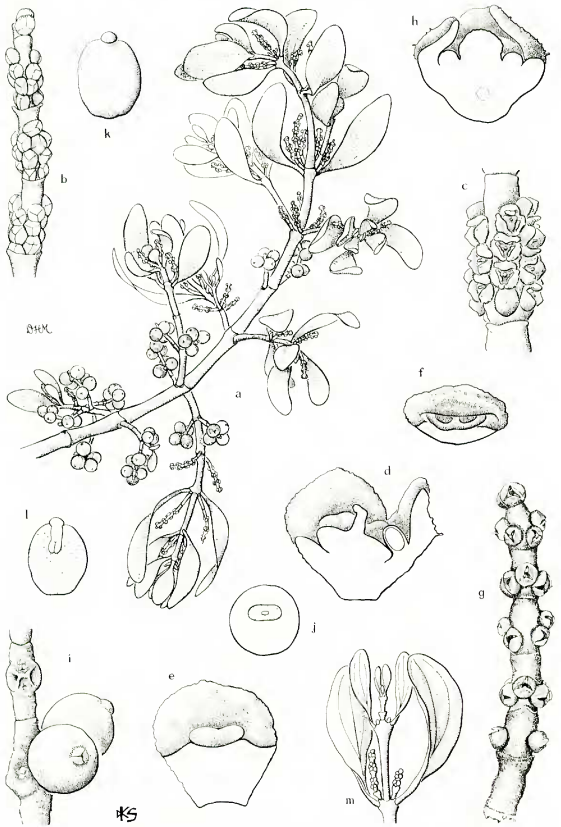

FIGURE 1. **Phoradendron.** a–l, *P. serotinum*: a, portion of carpellate plant with fruits on growth of the previous year and flowers on growth of the current year, × 1; b, tip of inflorescence before flowers have opened, × 8; c, detail of one fertile internode of staminate inflorescence with flowers at anthesis, × 12; d, staminate

1. **Phoradendron** Nuttall, Jour. Acad. Nat. Sci. Philadelphia II. **1:** 185. 1847.

Foliaceous [or squamate] shrubby parasites on the branches of woody angiosperms [or gymnosperms], with or without basal cataphylls on lateral branches. Absorptive organ a diffuse and anastomosing system of rootlike strands spreading out laterally into host cortex and phloem, giving rise to radial sinkers through phloem and into wood; secondary haustorial organs absent. Leaves [often] somewhat fleshy. Inflorescence 1–3 axillary [or terminal] spikes in which flowers are produced by intercalary action in 2 or 3 [to several] more or less regular longitudinal series, each resulting flower area topped by a single apical flower in a median position with regard to the bract. Flowers very small, 3- or 4-merous, imperfect [both staminate and carpellate flowers occurring on the same spike] or the plants dioecious. Staminate flower with a sessile, bilocular anther attached to the middle of each perianth segment, the flower terminated by a central cushion and papilla. Carpellate flower consisting of 3 perianth segments united with the unilocular ovary; ovules reduced to a central papilla within which 2 megagametophytes (embryo sacs) develop; stigma sessile, scarcely differentiated. Fruit a berry with 1, rarely 2, seeds consisting of endosperm with embryo and surrounded by viscous tissue. TYPE SPECIES: *P. californicum* Nuttall. (Name from Greek *phor*, thief, and *dendron*, tree, in obvious reference to the parasitism of the plant.)—MISTLETOE.

A large genus distributed from the United States to Argentina, the number of species vastly exaggerated in the only existing generic treatment (Trelease, 1916), which recognized 240. A large number of species have since been added, but it is probable that a reasonable revision of the genus would reduce the total to a hundred or fewer. The primary division of the genus into "Boreales" (lacking cataphylls) and "Aequitoriales" (bearing cataphylls), rank unspecified, seems, in the dim light shed by Trelease's monograph, to be generally workable. *Phoradendron* is closely related to—and often difficult to distinguish from—*Dendrophthora*, a strictly tropical genus (Kuijt, 1961).

A few species are present in the western United States, but only two occur in the Southeast. Of these, *Phoradendron rubrum* (L.) Griseb., a cataphyllous species reported by Cooley (1963) as a parasite on mahogany (*Swietenia Mahagoni*), although widespread in the West Indies, is restricted to south-

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flower in vertical section, one sessile anther shown in section to right, disc and sterile gynoecium in center, × 50; e, one perianth lobe removed from flower to show sessile anther, × 50; f, same, from above, to show dehiscence of anther by two apical pores, × 50; g, carpellate inflorescence, flowers open, × 8; h, carpellate flower in vertical section to show large disc and stigma, region of undifferentiated ovules indicated by circle of dots, × 50; i, detail of infructescence with two fruits, × 6; j, cross section of fruit, pericarp (?) unshaded, endosperm stippled, embryo in center of endosperm, × 12; k, seed, oriented as in fruit, × 12; l, seed in section, oriented as in "k," endosperm stippled, embryo unshaded, × 12. m, *P. rubrum*: tip of staminate plant with unopened flowers, × 2.

ernmost peninsular Florida, while *P. serotinum* (Raf.) M. C. Johnston (*P. flavescens* Pursh) has been variously interpreted as including certain western populations or as containing various species in both the eastern and southeastern United States. The view of Wiens is doubtlessly more reasonable in considering *P. serotinum* as a single species parasitic on a wide variety of dicotyledonous hosts in the area of the Generic Flora. Under this interpretation, *P. serotinum* is distributed from eastern Texas and eastern Oklahoma, eastward along the Gulf Coast to the Atlantic, southward to southernmost Florida, and northward and eastward to southeastern Missouri, southernmost Illinois, Indiana, Ohio, southeastern Pennsylvania, and southern New Jersey. Wiens treated the western populations formerly associated with this species as subspecies of either *P. villosum* (Nutt.) Nutt. or *P. tomentosum* (DC.) Engler.

The work of Baldwin and Speese and of Wiens makes it clear that, at least in the United States, the genus is characterized by a diploid chromosome number of 28. Baldwin and Speese were unable to discover chromosomal differences of any sort between 25 collections of *Phoradendron serotinum* from 15 different host species in Virginia and Arkansas. The considerable amount of damage (malformations, reduced growth rates, and increased predisposition to the attacks of certain insects and decay fungi) done to host trees needs no elaboration.

Baldwin and Speese found that meiosis occurs in staminate buds of *Phoradendron serotinum* in eastern Virginia in July and August. Flowering is in late autumn (October to late November in northern Virginia [Allard] and at least into January in Florida). Pollination of the minute flowers is by insects—presumably Hymenoptera, possibly wasps. Fruits mature the following fall or later, thus requiring up to a year and a half from flower primordium to maturation. The berries are eaten by various birds, which distribute the seeds. In contrast, the seeds of *Arceuthobium* are distributed explosively as the fruits break away from the pedicels. Initial velocities of the viscous-coated seeds may be 90 feet per second, and they may sometimes be thrown as far as 50 feet (see Hawksworth & Wiens, family references).

The superficial likeness of *Phoradendron serotinum* to the European *Viscum album* has made a transfer of the latter's folklore to North America easy. Most *Phoradendron* found on the northern markets at Christmas originates in Texas, New Mexico, Arizona, and Oklahoma, with some from Kentucky, Tennessee, and the Carolinas. The cities in the Southeast seem to draw upon more local sources. Dr. C. E. Wood reports, for example, that the *P. serotinum* sold in Roanoke, Virginia, is trucked in from Floyd, Franklin, and Suffolk counties, with some even from the Carolinas.

The poisonous berries of *Phoradendron serotinum* are mentioned under the family (see Hardin & Arena). Perkins and Payne note that "the berries and tea from the berries [of *P. serotinum*] have caused poisoning deaths of humans & livestock. Symptoms, which appear in 1–2 hours, are nausea, vomiting, profuse diarrhea, sweating, dilated pupils, rapid & labored respiration, shock & death due to cardiovascular collapse in about 10 hrs. Deaths have resulted from using the berries to procure an abortion." The foliage of *P. villosum* has poisoned cattle (Kingsbury).

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